Wilson Bulletin 117(4):336–340, 2005

AVIAN FRUGIVORY ON A GAP-SPECIALIST, THE RED ELDERBERRY (*SAMBUCUS RACEMOSA*)

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ABSTRACT.—In the temperate zone, few plants produce fruit during the peak of the avian breeding season when arthropods are abundant. This study examined avian frugivory on red elderberry (*Sambucus racemosa pubens*), a gap-specialist that fruits in late June and early July. First, we videotaped fruiting elderberry plants (n = 67 hr) within a forest to determine which avian species ate elderberry fruit. The birds that fed most frequently on red elderberry fruits were Scarlet Tanagers (*Piranga olivacea*) and Rose-breasted Grosbeaks (*Pheucticus ludovicianus*). We then analyzed radiotelemetry data for Scarlet Tanagers to determine (1) whether tanagers shifted their territories when elderberry was in fruit, and (2) whether tanagers traveled long distances off territory to visit fruiting elderberry. During the fruiting period, male tanagers shifted their home ranges and spent more time near elderberry bushes; however, they left their territories only 0.25 times per hr and moved an average of only 115 m during trips off territory. These results suggest that while tanagers do focus their activity near fruiting elderberry, they do not leave their territories regularly to find fruit. *Received 23 November 2004, accepted 18 July 2005.*

In the temperate zone, few plants produce fruit during the avian breeding season (Thompson and Willson 1979, Wheelwright 1988), and the typical pattern is for temperate zone plants to fruit in late summer and early fall (Morton 1973). Only a small fraction of the breeding bird community is even partly frugivorous, largely because of the high abundance and protein content of arthropods (although we note that many insectivorous migrants do eat fruit in the nonbreeding season). Little is known about the importance of fruit to temperate breeding birds (McCarty et al. 2002), or about the movements of territorial bird species in response to early-fruiting plants (Gorchov 1988).

Red elderberry (*Sambucus racemosa pubens*), typically found in forest gaps, is among the earliest woody plants to fruit in the northeastern region of the United States (Stiles 1980) and is available to forest birds while they are still nesting. In this study, we videotaped ripe elderberry shrubs to quantify which avian species fed on elderberry fruit and the rate at which plants were visited. We also analyzed radiotelemetry movements of one key species that eats elderberry, the Scarlet Tanager (*Piranga olivacea*)—to determine whether it shifts its territory use in response to fruiting elderberry or makes long distance movements off territory in search of fruit.

METHODS

Study area.—From 2000 to 2003, we studied avian frugivory on red elderberry at the Hemlock Hill Biological Research Area (41° 46′ N, 79° 56′ W), a 150-ha mixed forest in Crawford County, northwestern Pennsylvania. The fruiting period for elderberry was between mid-June and mid-July, although individual plants were sometimes depleted of fruit within 7–10 days of ripening in mid- or late June. We searched the study site for elderberry plants and found 54 different plants (0.36/ha) at 19 different sites (defined as >50 m apart; 0.13 sites/ha). Fruiting plants typically had 20–50 clusters of fruit per plant (mean = 24, SD = 25.8, n = 49 plants), with about 200 individual fruits per cluster. Fruits are brilliant red, small (3–5 mm diameter; 0.05 g wet mass), and have a relatively high-energy content (68.8 kcal/100 g; Usui et al. 1994).

Bird visits and bird surveys.—We selected medium- or large-sized elderberry plants for videotaping; for a subset of these plants, the mean number of fruit clusters was 46 (SD = 33, range = 8–105 clusters per plant, n = 11). Some sites contained several adjacent elderberry plants that were videotaped separately, but were considered the same site because presumably the same individual birds fed on adjacent elderberry plants. We videotaped 14 different sites, 3 of which were taped in 2 dif-

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TABLE 1. The occurrence of videotaped species foraging on red elderberry fruit (n = 17 sites) from mid-June to mid-July in northwestern Pennsylvania, and the detection of those species (percentage of sites) during bird surveys in early July 2003 at elderberry sites (n = 14). Foraging observations are based on the percentage of sites at which the species was videotaped and percentage of all bird visits (n = 106) to elderberry represented by that species.

Species	Elderberry foraging		Bird surveys
	% sites	% visits	
Scarlet Tanager (*Piranga olivacea*)	35.3	45.3	64%
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	23.5	22.6	36%
Red-eyed Vireo (*Vireo olivaceus*)	17.6	6.6	100%
Veery (*Catharus fuscescens*)	17.6	7.5	50%
American Robin (*Turdus migratorius*)	5.9	1.9	29%
Wood Thrush (*Hylocichla mustelina*)	5.9	0.9	79%
Northern Cardinal (*Cardinalis cardinalis*)	5.9	1.9	71%
Gray Catbird (*Dumetella carolinensis*)	5.9	5.7	21%
Eastern Towhee (*Pipilo erythrophthalmus*)	5.9	3.8	14%
Downy Woodpecker (*Picoides pubescens*)	5.9	1.9	—
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	5.9	0.9	—
Unidentified birds	29.4	8.5	

ferent years, yielding a sample size of 17 sites. Video cameras (Sony Hi-8) were positioned so that most or all of one fruiting plant could be observed, and we collected 1–4 hr of tape per taping session depending on the weather and the camera's capability. We videotaped plants between 09:00 and 17:00 EDT, only during dry weather. Tapes were later viewed on a television screen, and bird species were identified visually and/or by their call notes. We noted the time each bird spent foraging before departing from an elderberry plant. We could not accurately count the number of fruits eaten because our view of an individual was often blocked by vegetation as it foraged.

To assess the abundance of frugivorous species relative to their visitation to elderberry, in 2003 we surveyed 14 elderberry sites for the presence or absence of frugivores. At each site where fruiting elderberry was present, we listened for singing birds within 50 m of the elderberry site for 10 min. We then played back 1 min of song, followed by 1 min of silence, for nine species of passerines that are partially frugivorous (Red-eyed Vireo, Wood Thrush, Veery, American Robin, Northern Cardinal, Scarlet Tanager, Rose-breasted Grosbeak, Gray Catbird, Eastern Towhee; see Table 1 for scientific names). Surveys were conducted once during morning (09:00–12:00), from 30 June to 3 July 2003.

Radiotelemetry.—In 2000 and 2001, we captured tanagers by using a playback system, decoy, and mist nets and banded them with a federal band and a combination of individually identifiable color bands. Males (n = 10) were fitted with a small (1.4 g), BD-2G radio transmitter (Holohil Systems, Carp, Ontario, Canada) that was attached with a figure-8 harness made of cotton embroidery thread (see Rappole and Tipton 1991). The transmitter and harness together weighed about 5% of adult body mass (30 g). Transmitter batteries lasted 8 weeks and the range was approximately 1.5 km. The study site had conspicuous grid marks every 50 m and the locations of males were recorded by noting the closest grid mark(s) whenever the bird moved. Movements off territory were defined as occurring when a male entered another male's territory (for known boundaries) or when males moved at least 100 m away from their own territory boundary.

Tanagers were tracked between 13 May and 30 June to study off-territory movements (Fraser and Stutchbury 2004) and to compare movements before versus after elderberry fruit was ripe. We radio-tracked tanagers for about 2 hr at a time, between 06:00 and 14:00, and followed males from a distance of about 30 m. Observations were not made during wet weather because the receiver was not waterproof. We mapped the location of all elderberry shrubs in the territories of radio-tagged males, and quantified the relationship between territory size, movements, and fruiting shrubs.

We had a total of 116 hr of radio-tracking data—46 hr during the pre-fruiting period (before 15 June) and 70 hr during the fruiting period (15 June–30 June). We had a minimum of 6 hr of tracking time for each male used in our analyses.

For seven males we used paired observations (6 hr pre-fruiting, 6 hr fruiting) and predicted that males would spend more time in an area with ripe elderberries than they would during the pre-fruiting period. We used two measurements during the pre-fruiting and fruiting periods to determine whether males were more likely to include ripe elderberry patches during their movements: (1) the percent time spent within 25 m of an elderberry shrub out of the total time tracked, and (2) the total number of elderberry shrubs contained within the male's home range in each tracking session. Both comparisons were tested with a one-tailed, Wilcoxon paired signed-ranks test.

RESULTS

Birds that ate elderberry fruit.—From videotapes, we identified 11 bird species and one eastern chipmunk (*Tamias striatus*) foraging on ripe elderberry (Table 1). We were unable to identify the bird species in only 8.5% of visits seen on the videotapes. The Scarlet Tanager was the species observed most often on elderberry plants; tanagers were seen at 35.3% of sites, and accounted for 45.3% of all bird visits to elderberry. The Rose-breasted Grosbeak was the second most common visitor to elderberry (22.6% of visits). The occurrence of a given species feeding on elderberry did not correspond closely to the species' prevalence—as assessed during our site surveys (Table 1). The percentage of sites visited (r_s = 0.275, n = 9, P = 0.24) and the percentage of visits (r_s = 0.05, n = 9, P = 0.45) were not significantly correlated with the percentage of surveys on which the species was detected. For instance, Red-eyed Vireos and Northern Cardinals were very common birds at our study site (and responded readily to playback) but were rarely seen visiting elderberry shrubs. In contrast, the low level of frugivory by American Robins, Gray Catbirds, and Eastern Towhees likely did reflect the low abundance of these species in the forest. The Rose-breasted Grosbeak was often seen feeding on elderberry but was detected on only 36% of surveys, which may reflect a low detection ability for this species due to low song rates and weak responses to playback.

The rate of visits by frugivores was highly variable between sites. For sites that were observed for at least 3 hr (n = 10), we observed no visits at three sites, <1 visit/hr at three sites, 1–5 visits/hr at two sites, and >5 visits/hr at two sites. One elderberry plant was visited by birds 29 times over a 3-hr period, although this plant did not have an unusually large amount of fruit (84 clusters). For 2003, when we estimated fruit crop, there was no correlation between the total number of fruit clusters per site and the visit rate/hr at that site (r_s = 0.07, n = 7, P = 0.86).

The average time spent on elderberry per visit was 59.4 sec (SD = 55.2, range = 5–260 sec, n = 54 visits). Most birds consumed the small fruits while on the elderberry plant, although several species were occasionally observed feeding elderberries to their fledglings or departing with fruit in their bills (Scarlet Tanager, Rose-breasted Grosbeak, Veery, American Robin).

Elderberry effect on tanager movements and territory use.—We radio-tracked seven paired males during both the pre-fruiting and fruiting periods to determine whether they shift their home-range use in response to the presence of ripe elderberry fruit. During the fruiting period, males spent significantly more time <25 m from elderberry (12.8% ± 0.14 SD) than they did during the pre-fruiting period (4.0% ± 0.075; Z = −1.99, n = 7, P = 0.023). There also was a strong but nonsignificant trend (Z = −1.47, n = 7, P = 0.068) among males to shift their home ranges to include more elderberry shrubs during the fruiting period (1.71 ± 1.5) compared with the pre-fruiting period (0.71 ± 0.76). Territory size (ha) did not change significantly between periods (pre-fruiting: 0.64 ± 0.27, fruiting: 0.94 ± 0.60; Z = −1.014, n = 7, P = 0.16).

Eight of 10 males left their territories during the fruiting period, although the mean rate of off-territory forays was low (0.25 trips/hr ± 0.21 SD). In most cases, when males did leave their territories, they went only 115 m ± 124 (n = 8 trips) beyond their territory boundaries—roughly equivalent to the diameter of one tanager territory—and were not observed feeding on elderberry. We observed

only one male travel far (300 m) off territory to an area of ripe elderberry. In the 70.2 hr of tracking during the fruiting period, we observed 2 of the 10 radio-tagged males foraging on elderberry. In both cases, their mates (not radio-tagged) also were observed foraging on berries.

DISCUSSION

We observed 11 different species of birds feeding on elderberry. Of 33 passerine species that regularly breed in the forest at this study site (BJMS pers. obs.), 9 species were observed feeding on fruit, and all were already known to be partially frugivorous during the breeding season.

In some instances, we recorded high visitation rates to individual plants (10 visits/hr), but for most plants there were no, or only several, visits by birds each hour. Nevertheless, most plants were stripped of fruit by mid-July, suggesting that at some point birds (we assume) did consume the fruit. Denslow (1987) found that fruit removal rate (number of fruits removed per day) of red elderberry shrubs was significantly higher for isolated plants with large crops and for those with high sugar content in the fruit. We found no correlation between number of fruit clusters per site and bird visitation rate, although our sample sizes were modest. For instance, one site with nine different elderberry shrubs and 198 fruit clusters was not visited in 3.5 hr of observation. Another site had only a single elderberry plant with 84 fruit clusters, yet it was visited 9.6 times per hr.

The occurrence of a given species foraging on elderberry did not closely correspond to its prevalence in the forest (Table 1). Wood Thrushes were rarely seen on elderberry shrubs, despite this species being detected at 80% of elderberry sites during bird censuses. Similarly, Red-eyed Vireos and Northern Cardinals were present at most elderberry sites but represented only a small fraction of all bird visits to elderberry shrubs. The species-specific use of elderberry fruit could reflect differences in availability of insect prey to birds with different bill morphologies and foraging substrates, and hence the relative value of the fruit at a time of year when many adults are feeding offspring.

Almost half the visits to elderberry during our videotaping were made by Scarlet Tanagers. Although male tanagers did not make long trips off territory to find fruit, they did spend more time near elderberry when it was ripe. However, stomach content analysis of forest thrushes revealed relatively low fruit content in June and July (White and Stiles 1990), and the same may be true for tanagers (Mowbray 1999). The low fruit content in the diet could reflect the low number of fruiting species available at that time of year and the low density of these plants. In our study area, the density of elderberry sites was only 0.13/ha and many tanager pairs had no elderberry plants on their territories. We have observed tanagers feeding elderberries to older nestlings and fledglings, but it is not known whether feeding fruit to young increases the reproductive success of the parents.

Our results have implications for understanding seed dispersal by this early-fruiting plant. One of the potential costs of early fruiting is limited seed dispersal due to territoriality during the peak breeding season of birds (Morton 1973, Willson and Thompson 1982). However, Gorchov (1988) found that dispersal of one early-fruiting species, *Amelanchier arborea*, was not restricted by territoriality, because the main avian disperser was the Cedar Waxwing (*Bombycilla cedrorum*), which forages in flocks. Our results suggest that dispersal distance of red elderberry within a forest may indeed be limited by territoriality because male Scarlet Tanagers did not regularly commute off territory to search for fruit. Most of the birds that ate elderberry (Table 1) defend all-purpose territories and may be similarly constrained. Although male (and female) tanagers do often leave their territories after breeding (Vega Rivera et al. 2003), this occurs later in summer after the main fruiting period of red elderberry. Red elderberry is a gap-specialist, but it is not necessarily disadvantaged by dispersal within a bird's territory. What may be more important than distance *per se* is that the seeds are dispersed to a favorable site (e.g., Wenny and Levey 1998)—in this case, another gap within the territory—or are dispersed to sites within the forest where they can wait for a gap to form above them.

ACKNOWLEDGMENTS

We thank Hemlock Hill Biological Research Area and all the landowners for permission to conduct re-

search there. This project was funded by awards to BJMS from the Molson Foundation, the Premier's Research Excellence Award, and the Natural Sciences and Engineering Research Council of Canada. K. J. Cooper, R. Norris, M. Ortwerth, and M. Williams all provided excellent field assistance. Special thanks go to M. Ortwerth and K. J. Cooper for their hard work. E. S. Morton, D. J. Levey, B. Woolfenden, and three anonymous reviewers provided comments on the manuscript.

LITERATURE CITED

Denslow, J. S. 1987. Fruit removal rates from aggregated and isolated bushes of the red elderberry (*Sambucus pubens*). Canadian Journal of Botany 65:1229–1235.

Fraser, G. S. and B. J. M. Stutchbury. 2004. Area-sensitive birds move extensively among forest patches. Biological Conservation 118:377–387.

Gorchov, D. L. 1988. Does asynchronous fruit ripening avoid satiation of seed dispersers? A field test. Ecology 69:1545–1551.

McCarty, J. P., D. J. Levey, C. H. Greenberg, and S. Sargent. 2002. Spatial and temporal variation in fruit use by wildlife in a forested landscape. Forest Ecology and Management 164:277–291.

Morton, E. S. 1973. On the evolutionary advantages and disadvantages of fruit eating in tropical birds. American Naturalist 107:8–22.

Mowbray, T. B. 1999. Scarlet Tanager (*Piranga olivacea*). The Birds of North America, no. 479.

Rappole, J. H. and A. R. Tipton. 1991. New harness design for attachment of radio transmitters to small passerines. Journal of Field Ornithology 62: 335–337.

Stiles, G. W. 1980. Patterns of fruit presentation and seed dispersal in bird-disseminated woody plants in the eastern deciduous forest. American Naturalist 116:670–688.

Thompson, J. N. and M. F. Willson. 1979. Evolution of temperate bird/fruit interactions: phenological strategies. Evolution 33:973–982.

Usui, M., Y. Kakuda, and P. G. Kevan. 1994. Composition and energy values of wild fruits from the boreal forest of northern Ontario. Canadian Journal of Plant Science 74:581–587.

Vega Rivera, J. H., W. J. McShea, and J. H. Rappole. 2003. Comparison of breeding and postbreeding movements and habitat requirements for the Scarlet Tanager (*Piranga olivacea*). Auk 120:632–644.

Wenny, D. G. and D. J. Levey. 1998. Directed seed dispersal by bellbirds in a tropical cloud forest. Proceedings of the National Academy of Sciences USA 95:6204–6207.

Wheelwright, N. T. 1988. Fruit-eating birds and bird-dispersed plants in the tropics and temperate zone. Trends in Ecology and Evolution 3:270–274.

White, D. W. and E. W. Stiles. 1990. Co-occurrences of foods in stomachs and feces of fruit-eating birds. Condor 92:291–303.

Willson, M. F. and J. N. Thompson. 1982. Phenology and ecology of colour in bird-dispersed fruits, or why some fruits are red when they are "green." Canadian Journal of Botany 60:701–713.